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Published in:
Wader Study Group Bulletin

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2005

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Robinson, R. A., Clark, N. A., Lanctot, R., Nebel, S., Harrington, B., Clark, J. A., Gill, J. A., Meltofte, H., Rogers, D. I., Rogers, K. G., Ens, B. J., Reynolds, C. M., Ward, R. M., Piersma, T., & Atkinson, P. W. (2005). Long term demographic monitoring of wader populations in non-breeding areas. *Wader Study Group Bulletin*, *106*, 17-29.

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Long term demographic monitoring of wader populations in non-breeding areas

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Keywords: shorebird, population trends, survival, productivity, conservation.

Understanding numeric changes in wader populations requires knowledge of the demographic parameters underlying such changes, i.e. survival and recruitment. Data from long-term monitoring programmes are crucial for obtaining these parameters. Following discussions held at a workshop on demographic monitoring of wader populations at the 2004 International Wader Study Group meeting, we present guidelines for establishing new programmes to monitor survival and recruitment of waders in non-breeding areas, particularly those species that breed in the Arctic. We provide a general overview of some common issues in the demographic monitoring of waders and then provide detailed methods for measuring both recruitment and survival on the non-breeding grounds.

INTRODUCTION

Worldwide there is much concern over the high proportion of wader (shorebird) species that are declining, particularly amongst arctic-breeding species (e.g. IWSG 2003, CHASM 2004). To fully understand why these changes are occurring, it is necessary to understand how and why the underlying demographic parameters (recruitment and survival) of a population are changing, both temporally and spatially. Such an understanding requires long-term demographic monitoring programmes. For some species (mostly temperate breeders) these programmes are readily established on the breeding grounds, but for arctic species, monitoring breeding birds poses immense logistical difficulties, so monitoring on the non-breeding grounds may be required. For such monitoring to be effective, however, clear methodologies, comparable between species and regions, need to be established.

Following a workshop on arctic waders, climate and monitoring in Denmark in December 2003, the Committee for Holarctic Shorebird Monitoring (CHASM) was established (CHASM 2004). Subsequently, CHASM organised a workshop to discuss issues and methodologies surrounding the demographic monitoring of waders at a meeting of the International Wader Study Group in Germany in November 2004. The workshop focused particularly on those species that breed in the Arctic, where monitoring is logistically difficult. This paper is based on those discussions and provides guidelines on issues to be considered when establishing new projects. It is hoped that this will stimulate discussion of such methods and provide a greater appreciation of some of the difficulties that might be encountered. We focus on demographic monitoring of birds in their non-breeding ranges; a companion paper is being prepared that provides a discussion of monitoring birds on their arctic breeding grounds (Lanctot *et al.* in prep.).

WHY DO WE NEED DEMOGRAPHIC MONITORING?

Essentially, populations change as a result of variation in productivity or survival of individuals (e.g. Boyd & Piersma 2001). Immigration and emigration are largely irrelevant at a population level, but might need to be accounted for at a local level if distribution patterns are changing, for example, as a result of climate change or human disturbance. It is necessary to monitor changes in the two key demographic parameters (productivity and survival) as well as changes in population numbers to fully understand the causes of population change, and for planning effective management (e.g. Goss-Custard 1996, Green 1999, Fox 2003). Long-term population monitoring is also required to diagnose population declines and ascertain whether the magnitude of the declines is sufficient to warrant conservation concern; studies lasting only a few years may confuse short-term variation with population trend. Long-term monitoring can also help in identifying sites of conservation importance and may form part of international commitments (e.g. Stroud *et al.* 1990, Pienkowski 1991).

Longer-term changes in survival or productivity may be evident before changes in population numbers and signal a potential change in conservation status. Changes in environmental conditions may have an impact on demographic parameters directly, for example reduced food availability may lower survival and hence result in a fall in population numbers. Demographic monitoring can therefore be an early barometer of future population change (e.g. Monaghan *et al.* 1989), as there may be significant breeding population buffering in long-lived species due to the presence of non-breeding individuals (e.g. Piersma & Baker 2000, Bruinzeel 2004), which may delay impacts on breeding population size. Demographic monitoring can identify the critical life-cycle stage(s) on which environmental factors are operating to cause population change, and exclude others which are less relevant, by identifying the primary cause for population change (e.g. Green 1999, Piersma & Lindström 2004). Monitoring also provides useful information on average demographic rates both to identify normal levels for the demographic rate, though these may be population specific (e.g. Stroud *et al.* 1990), and to provide information for broader ecological models and adaptive management programmes (e.g. Perrins *et al.* 1991, Nichols 1991, Stillman *et al.* 2001).

MONITORING DEMOGRAPHIC PARAMETERS

Long-term monitoring programmes have a venerable history in the field of ornithology (e.g. Dunnet 1991, Perrins *et al.* 1991). Developing such a programme to provide useful information can be fraught with difficulties, not least because projects are usually not envisaged to be long-term in the beginning (e.g. Krebs 1991, Bearhop *et al.* 2003). Although waders are popular study organisms, long-term studies of population dynamics and even simple monitoring of numbers are few (Thompson & Thompson 1991). Consequently, there still remain significant gaps in our knowledge and understanding of wader population trends (Piersma *et al.* 1987, Delany & Scott 2002).

Waders are generally long-lived birds, with longevity records for most exceeding ten years and some larger species living more than thirty years. This is a consequence of high annual survival (often 70–90% in adults), but populations can be quite sensitive to changes in survival even if it occurs over only a short period (e.g. Goss-Custard *et al.* 1996, Hitchcock & Gratto-Trevor 1997, Boyd & Piersma 2001). Information on mortality causes may be gathered from, for example, surveys of beached birds (e.g. Camphuysen *et al.* 1996), but monitoring survival requires the fate of individual birds to be known. This requires applying individually identifiable marks, to a representative sample of individuals in the population. Usually waders are marked with either individually numbered metal leg rings that can be read when the bird is re-caught or found dead (Appendix 1), or colour marks that can be read from a distance (Appendix 2). For monitoring survival (and recruitment from recapture histories) individually identifiable combinations are required; there are very few situations where cohort or group marking is preferable to individual marking.

Survival, however, can differ between breeding, non-breeding and migratory periods, requiring the synthesis of information collected across the annual cycle (Lank & Nebel *in press*). Examples among waterbirds are provided by studies of individually marked geese. For some populations, rates of daily survival were lower during migration than during breeding or non-breeding periods (Owen & Black 1991, Clausen *et al.* 2001), possibly as a consequence of hunting (Ward *et al.* 1997). Other studies have documented lower survival rates during the breeding seasons, or concluded that breeding, wintering, and even migration seasons had similar rates of natural mortality (Gauthier *et al.* 2001, Madsen *et al.* 2002).

Production of young, and hence recruitment into the adult population, can vary greatly between years, particularly amongst high Arctic species, where weather conditions, the abundance of predators and their alternative prey appear to be important factors (Summers & Underhill 1987, Blomqvist *et al.* 2002). Moreover, there can be strong spatial variation in nesting success (McCaffery & Ruthrauff 2004, Soloviev & Tomkovich 2004). Monitoring productivity for temperate species on their breeding grounds is typically more straightforward, but even for these species it can be hard to be certain of the proportion of chicks that survive to fledging and recruitment into the breeding population is even more difficult to quantify. For populations of Arctic breeding birds ascertaining fledging rates may be unrealistic as these species generally breed at low densities and are highly dispersed over remote Arctic tundra (e.g. Seebohm 1901, Meltofte 1985, Bart & Earnst 2002).

For waders, we may be interested in recruitment into two different sub-populations. Firstly, we may monitor the number of juvenile birds entering the non-breeding population (Minton 2003, Clark *et al.* 2004). This can be estimated from the proportion of juvenile birds present in non-breeding flocks, either from visual observation (Appendix 3), or in caught samples (Appendix 4). Recruitment into the non-breeding population is a measure of productivity, though it also includes components of mortality prior to fledging and from the first southward migration (Boyd & Piersma 2001, Underhill *et al.* 1989, Harrington unpubl.). An alternative to catching or watching mixed flocks may be to count numbers of juveniles in particular areas or habitats where only juveniles are known to occur (Appendix 3). This may be particularly relevant during the southward migration where adults and juveniles often occur at different times and in different areas or habitats, either at local or regional scales (e.g. van der Have *et al.* 1984, Meltofte 1993, Nebel *et al.* 2002). This may be helpful for assessing numbers in each age-class, but can give rise to difficulties when comparing recruitment between different non-breeding areas.

Demographically, the critical recruitment parameter is of birds into the breeding population. Such recruitment can be determined using recapture histories of ringed birds from the adult population (Appendix 5, Pradel *et al.* 1997). Traditionally, recapture histories are used as a way to measure the frequency with which birds leave the population (i.e. mortality, including emigration in open populations). Consideration of the recapture histories in reverse gives a measure of the number of birds entering the population (i.e. recruitment). This, however, is recruitment into the marked population, which may be equivalent to the breeding population, but for species where age at first breeding is delayed by one or more years, as in many species which spend the boreal winter in the southern hemisphere, then the two will not be equivalent unless non-breeders can be identified (Minton 2004).

Demographic monitoring is of most use when used in combination with counts in an integrated framework (e.g. Baillie 1990). Such integrated monitoring can help to understand the causes of population declines and to inform management decisions (Peach *et al.* 1994, Goss-Custard 1996, Atkinson *et al.* 2003). New methods are being developed which allow consideration of demographic and census data in one analysis, which should provide for improved understanding of population processes (e.g. Brooks *et al.* in press)

GENERAL CONSIDERATIONS FOR MONITORING PROGRAMMES

There are a number of problems that need to be considered when initiating monitoring studies of wader populations that relate both to bird behaviour and distribution and also to logistics and the availability of personnel. We discuss such general issues briefly here, as they apply in most situations, and draw attention where there may be particular problems in the accompanying guidelines (Appendices 1–5).

Few long-term monitoring programmes start as such, but it is always worth thinking about data that could be collected for future use, since it is usually impossible to gather data retrospectively. In an ideal world, all monitoring programmes would be designed on the basis of sound statistical principles with appropriately stratified random sampling and sufficient sample sizes determined from prior power analyses (Bart *et al.* 2000). In a pragmatic world, monitoring programmes rely on harnessing the efforts of (often pre-existing) local groups and enthusiasts in collaboration to derive information on the parameters of interest. These approaches may be illustrated by the Program for Regional and International Shorebird Monitoring (PRISM) and International Shorebird Survey (ISS) programs in North America, both of which aim to monitor Arctic breeding waders, but which use very different approaches. PRISM uses a designed sampling program to ensure estimates are as unbiased as possible in response to the needs of the US Shorebird Conservation Plan (Skagen *et al.* 2003), whereas the ISS relies on a network of volunteers counting local sites. The budgetary requirements of PRISM are large, and it is questionable whether such a program could be supported elsewhere, and for how long it can be maintained. An evaluation of the relative reliability of the results of each approach would be illuminating when sufficient results are available. While more 'ad hoc' approaches are useful, they should not ignore the statistical complexities present when monitoring wader populations; conversely, survey designs should not be so complex or intensive that fieldworkers will have difficulty sustaining comparable effort.

All monitoring requires the production of summary statistics to synthesize the mass of field observations. To condense information into a manageable number of figures (usually an average with an associated measure of error), it is necessary that the data collected have certain properties to allow meaningful calculation of the summary statistics. Perhaps the most important of these properties (or assumptions) is that the birds measured (the sample) are representative of the population of interest, so conclusions drawn from the sample may be applied to the population as a whole. A second consideration, which is particularly important for survival monitoring, is that individuals need to behave independently of each other. Thirdly, most analyses assume that birds are distributed randomly, which is unlikely to be true in any real situation (e.g. Harrington & Leddy 1983, Durell & Atkinson 2004). In most cases, data collected from wader populations will not conform, to a greater or lesser extent, to all of these assumptions. The challenge then, is to understand the reason why the assumptions are not met, and include this in the analytical procedure. Although this at first may seem daunting, it usually gives clearer results and a better understanding of the biological processes involved.

The importance of population structure

Perhaps the greatest difficulties in obtaining a representative sample stem from the fact that wader populations exhibit much heterogeneity in their distribution. Many of the more advanced statistical techniques are designed specifically to deal with such problems to yield meaningful estimates of the parameter of interest and its associated error. Such error measurements are vital, both to give a guide to the confidence we may have in the estimate, but also to allow meaningful comparison between different estimates, either through time or between different studies. There has been much development recently of user-friendly software to perform such analyses (e.g. MARK, White & Burnham 1999), but even these sophisticated programs require a carefully designed sampling protocol with sufficient sample sizes (e.g. Baker *et al.* 2004).

It is obvious that waders do not occur randomly in the environment, either at a global, regional or local scale. At a global scale, most wader species are more or less segregated into relatively discrete (though overlapping) populations, often in relation to particular flyways (Davison & Pienkowski 1987, Piersma & Lindström 2004). Within flyways, however, flocks of individuals present in staging or non-breeding areas may represent individuals from multiple populations or may show a bias towards a particular age or sex. Identifying the population an individual comes from may be extremely difficult, particularly when no distinguishing plumages or biometric differences exist. In the last few years, technical advances in genetics (Wennerberg 2001), stable isotope analyses (e.g. Hobson 1999, Atkinson *et al.* in press) and multi-element analyses (e.g. Szep *et al.* 2003) are allowing the breeding origins of birds in non-breeding areas to be determined.

At a regional, or estuary, level there are likely to be unequal movements between (sub) sites, even though these sites may be geographically close (e.g. Burton 2000). Within sites, birds will not be distributed randomly as birds feed and roost in different areas, and individuals adjust where they forage in relation to a number of factors (e.g. Hilton *et al.* 1999). Birds can often be extremely site faithful (Ens & Goss-Custard 1986, Ens & Cayford 1996) and some individuals may even hold exclusive territories (e.g. Townshend 1985, Turpie 1995). Juveniles will often occur in the poorer habitats, and may use foraging areas when adults are roosting. Even within flocks, birds may occur non-randomly, with immature birds often on the outside of flocks (e.g. Harrington 2004, Rogers *et al.* in press).

Faced with such heterogeneity, an early step in any analysis should be to ascertain how well the proposed statistical model fits the data to hand. When all assumptions are met, the sum of deviations between the observed data and the model fitted values will be proportional to the sample size (in fact, the ratio of total deviance to degrees of freedom should approximate unity). Ecological data are seldom perfect, however, and ratios of two to three, indicating some breaking of the modelled assumptions are not uncommon (Anderson *et al.* 1994). Such lack of fit is probably not too serious and can be accommodated in the modelling process by the inclusion of an overdispersion factor or calculation of quasi-likelihood statistics (e.g. qAIC) to account for the extra (unmodelled) variance present (Crawley 1993, Anderson *et al.* 1994). Failing to do so will lead to an underestimation of the error about the parameter estimates. If the deviance : degrees of freedom ratio is greater than 2–3, then the assumptions underlying the model do not hold well and thought needs to be given to identifying a more appropriate model to account for the unexplained heterogeneity as the statistics produced may otherwise be misleading. Where goodness of fit tests fail, stratifying the data, or better the sampling, by site, habitat, age or sex, for example, is likely to be helpful.

Long-term changes

The potential effects of habitat or other behavioural changes should be taken into account when designing monitoring programmes and interpreting data generated by them. In long-term data sets habitat changes over the study period may pose problems. Adult and juvenile waders often have different habitat preferences, and any development in the direction of, for example, more or less muddy substrates will potentially influence the age structure of the birds utilising the site be it for staging or wintering (e.g. Meltofte 1987). Climatic conditions play a large part in determining where individuals spend the non-breeding period and long-term changes in climate are likely to lead to range shifts (Austin & Rehfisch 2005), potentially altering the age (etc.) distribution at individual sites.

Over the past two decades, a population of shorebirds drastically decreased their usage of a small stop-over site in south-western Canada, while no change was detected at a larger site close by (Ydenberg *et al.* 2004). Smaller sites are considered more dangerous, and the observed change in habitat use was interpreted to be the consequence of increased abundance of Peregrines *Falco peregrinus*, which have been recovering worldwide after the extensive use of DDT during World War II. Understanding such changes may be necessary to understand the population dynamics of the shorebird (e.g. Whitfield 2003).

Setting priorities

Before starting any monitoring project it is important to be clear about the aims of the project and to ensure there are sufficient resources to make it sustainable. Given limited resources, it is obviously impossible to monitor everything, thus priorities need to be set. For sites, the importance of the site at both local and flyway levels needs to be assessed for the species present, as well as the ease with which the chosen species may be monitored reliably (see Appendices 1–5). For species-based monitoring, sites need to be identified which will produce reliable results. Where several groups are working on the same species, it is important to foster links and communication, so that schemes are both comparable and complementary. Lack of funds or personnel, especially in countries with limited financial resources, may require studies to be focussed on imperilled or declining species, but it is important not to neglect those species that are presently abundant; these may be the conservation priorities of the future.

In any study, it is important to have an understanding of the mobility of birds using the site. Ideally, the site will be an area, with limited environmental heterogeneity, where a non-breeding population arrives over a defined (short) period and remains relatively self-contained until the return northward migration. Further, the population in question should ideally come from a single breeding population, or, at least, from an identifiable mix of populations. In most cases, this is clearly unrealistic, so compromises have to be made. Species are likely to be easier to monitor in non-breeding areas outside the passage period, where the population tends to be more stable than in staging areas, unless an estimate of turnover can be made (e.g. Schaub *et al.* 2001). It is also likely that the best areas in a flyway for monitoring will be species specific.

Sample sizes are an important consideration in designing any study. When quantifying age ratios (Appendices 3 and 4), multiple samples of 30–50 birds or more are likely to be required to achieve reasonable estimates; although if all eleven birds present at a site are juvenile then there is little doubt that the local age-ratio is 1 (though this is no longer a sample). For measuring survival (Appendices 1 and 2) and recruitment from life-histories (Appendix 5), re-encounter rate, either through sighting or catching, is more important than the number of birds ringed (Fig. 1). For estimates with reasonable precision, in excess of 50 birds re-encountered per observation period are likely to be necessary. Where these sample sizes are not achievable, biologists should consider whether the reduced precision makes the monitoring useful. In some cases low sample sizes may not negate the usefulness of a study, particularly in areas where information is poor, or lacking. For general monitoring it is probably better to sample individuals from a number of small catches/flocks in several locations rather than a few big catches/flocks at one location, as this averages over different site conditions and may reduce bias due to local heterogeneity. However, such heterogeneity should be carefully considered when it comes to interpreting the results.

Sampling and data logistics

Successful monitoring requires dedication and commitment from the individuals involved, where the long-term effort is patchy, data may not be analysable, wasting valuable effort (Bearhop *et al.* 2003). Most monitoring is carried out by unpaid enthusiasts, so a realistic assessment of the level of activity that is likely to be sustainable over several years is essential. There may be a number of ways of monitoring a

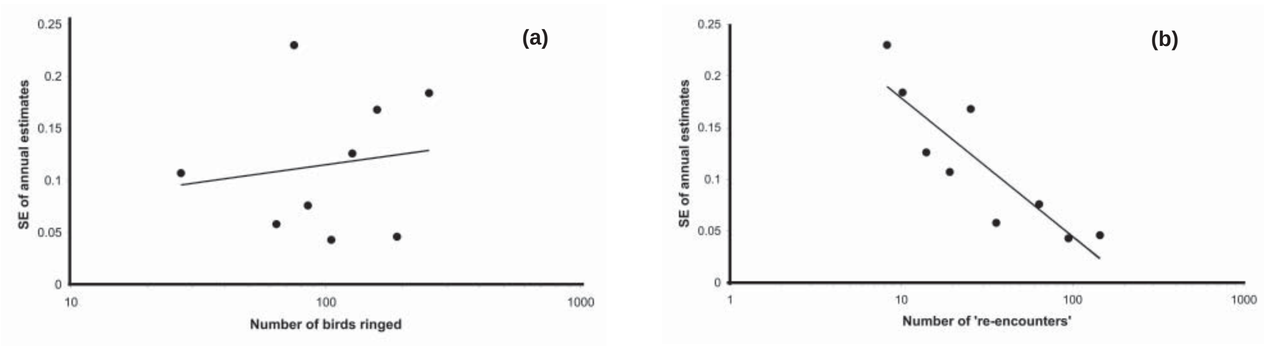

Fig. 1. Precision of survival estimation (expressed as mean standard error of the annual estimates) in relation to (a) the average number of birds ringed each year ($R^2 = 0.02$) and (b) the average number re-trapped or re-sighted each year ($R^2 = 0.76$). Useful estimates of survival are typically those with a standard error of 0.05 or less. Studies included used colour mark re-sighting (5) or re-traps of metal-ringed birds (4).

particular parameter, for instance, monitoring of age-ratios may be done through visual observation of flocks (Appendix 3), or from caught samples (Appendix 4). The former requires only one or two people, whereas catching birds, typically by cannon netting or erecting large arrays of mist nets requires a large team of people. The two methods appear to give similar measures (e.g. Rogers *et al.* in press), so programmes should be tailored to the available resources and the time of year at which they can be achieved successfully. An absolute minimum for long-term monitoring is five years (for shorter time series it is difficult to evaluate normal annual variation), however, the value of the data increases greatly if the study continues for much longer.

Securing data and making it available for the long-term is an important consideration for any new study, especially for waders, whose migratory flyways span countries and continents. International co-operation and standardisation of data are required to fully understand population processes. It is important that data collection occurs in a manner that is comparable between groups and research teams, and that data are collected and stored in a manner that is easily transferred to facilitate co-operative analyses (e.g. Brouwer *et al.* 2003). Thought should also be given to securing the data for the long-term. There have been many cases where data collected for one purpose are later found to be useful for historical comparisons (e.g. Lehikoinen *et al.* 2004) and cases where data have been lost when research programmes finish or key personnel leave. Consequently, a necessary first-step is the establishment of a central database so that valuable data are not lost but remain available for future analyses.

FUTURE DEVELOPMENTS

It is clear from the above that many challenges remain in wader demographic monitoring, however, a number of general areas emerge where further work would be useful.

Waders, perhaps more than most birds, tend to exhibit extreme heterogeneity of distribution, with age, sex, location, habitat, disturbance and food availability being amongst the key determinants. This clearly makes for more difficult statistical analysis and interpretation of results. These obstacles can often be overcome by stratification of data or by designing appropriate sampling programs that take these factors into account. Wader biologists should not shy away from such complications, as it is necessary to consider these factors in producing robust and reliable figures, which may be used outside the sphere of the original work, and which may also generate useful biological insights. Rather, efforts should be made to bring statistically minded workers and field biologists together, both to analyse individual datasets and to develop generally applicable techniques for such problems. Waderologists need to embrace heterogeneity!

In addition to developing statistical techniques, fieldworkers would benefit from further development of software to allow them to analyse their data relatively painlessly. A particular area where development would be useful is in the fitting of multi-strata models, which are often necessary to adequately account for heterogeneity in wader populations. Some important recent advances have been made here (Choquet *et al.* 2003), although the blind application of complex statistical techniques without a clear understanding of their underlying assumptions may lead to biased or even misleading conclusions. Again a dialogue between statisticians and fieldworkers is required to ensure greatest benefit from future developments.

In many cases, re-sighting of colour marked birds may provide information on demographic parameters with greater precision from a smaller number of birds than is possible from recapturing ringed birds. Colour marking has been used for many years and it is becoming difficult to develop new scheme combinations. The use of coloured flags, particularly those inscribed with a unique combination of characters, offers great potential for enabling individual identification of birds in the field using a minimum of marks (which should also reduce reading errors), though a reasonably close approach to birds is still required. However, it is essential that there is international co-ordination of such schemes, particularly within flyways and in areas where flyways overlap (e.g. Myers *et al.* 1983, Townshend 1983). The infrastructure for such central registration already exists (Table 1), and it is important that wader biologists are made aware of it and participate fully. Further consideration of the plastics used, bearing in mind the harsh environments experienced over the (potentially) long life of many wader species, would be useful to minimise problems of flag loss over time.

Although colour marking offers great potential, it should not mean the neglect of national ringing programmes, which fulfil a very important role. Metal ringing schemes, which are usually run on a national or international scale, are able to provide information at a much larger scale than colour-marking schemes, which often tend to be more spatially focussed for logistical reasons. However, greater structure

Table 1. Details of international colour marking schemes within each of the major flyways.

Flyway		
Pan-American	Contact:	cheri.gratto-trevor@ec.gc.ca
	Protocol:	www.mb.ec.gc.ca/nature/migratorybirds/pasp/index.en.html
	Sightings:	www.mb.ec.gc.ca/nature/migratorybirds/pasp/dc29s01.en.html
Afro-European	Contact:	wsg@bto.org
	Protocol:	Not available
	Sightings:	www.ring.ac
Middle Asian		None operating
East Asian-Australasian	Contacts:	See www.tasweb.com.au/awsg
	Protocol:	www.tasweb.com.au/awsg/protocol.htm
	Sightings:	www.tasweb.com.au/awsg/legflag/report.htm

and focus within such ringing programmes, with an aim to improve long-term monitoring is to be encouraged (e.g. Minton 2003). It is also important that, where possible, data from monitoring schemes should be submitted to, and included in national databanks, both to facilitate collaborative analyses and to provide data security.

A major challenge in understanding wader distribution and population processes stems from the mixing of multiple populations within sites, a characteristic that can also vary temporally. Further development of methods to identify breeding population origin of individuals in non-breeding areas would lead to great advances in our knowledge of wader biology. They would also be a great help in addressing some issues of heterogeneity in analyses, as well as providing insights into the link between breeding, passage and non-breeding areas, which can have important consequences for the reproductive and survival potential of individuals (e.g. Gunnarsson *et al.* 2004).

ACKNOWLEDGEMENTS

We thank the participants of both the Karrebäksminde, Denmark (2003) and Papenburg, Germany (2004) workshops for discussion on this topic and CHASM for providing the stimulus for writing this paper. We thank John Goss-Custard for commenting on our manuscript. We are also extremely grateful to the legion of volunteers, without whose tireless efforts monitoring of waders would probably be impossible.

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APPENDIX 1. MONITORING SURVIVAL: METAL RINGING

Summary

Outline of method

This method relies on catching a large sample of birds and fitting them with uniquely numbered metal rings, which are later recovered through subsequent recaptures or reports from birds found dead.

Advantages

This method can be used on all species that can be caught in large numbers and is particularly suitable for studies with large geographic scope. The effort needed to capture birds is often intense, but only for short periods. Survival rate estimates may be subject to fewer sampling biases than colour-mark studies (Appendix 2).

Disadvantages

The method requires large numbers of birds to be sampled and accessible and suitable sites for catching birds. Such sites may not be used by the entire population, giving rise to potential biases. Sampling programs are vulnerable to outside influences, such as adverse weather and require large teams to deal with initial and subsequent catches. Furthermore, band recovery rates are often low.

Method

Birds are caught, usually with cannon or mist nets and are fitted with a uniquely numbered metal ring with a return address. This ring should be made of a durable metal (e.g. stainless steel or incoloy); aluminium rings are not recommended, particularly for long-lived species on which even incoloy rings have to be replaced at regular intervals. Survival rates may be estimated either from subsequent recaptures of birds at the site, or from reports of birds found dead (or shot, which have a very different spatial distribution).

Site characteristics

The site needs to support a sufficient number of birds, ideally large flocks. For cannon netting, flocks need to be concentrated in a small area to make catching efforts worthwhile. Non-breeding high tide roosts are ideal for this purpose. High turnover of birds can create problems, as individual birds will not have equal re-capture probabilities. With cannon netting, public safety and education issues need to be carefully considered. Mist netting does not require such concentrations of birds, but birds need to move predictably within the area; the tide edge or tidal pools in coastal locations or sewage farms inland are typical examples. Flocks can also be encouraged into the vicinity of nets using tape lures (Clark & Austin in prep.). If catches are made on multiple sites, the method and pattern of catching on each site should be similar between years, to avoid problems with recapture heterogeneity (particularly important where live recaptures are being considered).

Sampling period

Survival analyses using ringing data require equal probabilities of catching each bird, therefore it is best used where stable flocks are reliably present across years. This usually equates to non-breeding roosting flocks outside the passage period. The timing of migration typically varies with location, hence optimum catching times should be determined locally to avoid significant emigration and immigration of birds into the study areas. November to February is a commonly chosen period. Strictly, most analytical methods require the capture period to be instantaneous, or at least very short relative to the re-capture period, though in practice models are relatively robust to violations of this assumption, particularly if the pattern of catch effort does not vary much between years (Smith & Anderson 1987).

Minimum annual sample size

As recovery rates are low, a large number of birds need to be ringed on an annual basis. In small populations, one should strive to maintain a large proportion of the population as marked. In general, the precision of survival estimates is influenced to a greater extent by the number of recovery events than the number of birds ringed. To achieve reasonably precise survival rate estimates, around 50 recaptures or recoveries a year should be regarded as a minimum for estimating annual survival rates, more would be preferable (Fig. 1). The recapture rate will depend on a combination of the survival rate, site fidelity and catching effort.

Resources required

A large team of people, with a high time commitment, are likely to be required to catch sufficient numbers. For cannon netting, suitable permissions and clearance may be required to ship and use the required explosive charges, and additional permission may be required from the owner of the ringing site; it is important that such permission will be available on an ongoing basis.

Data analysis

There are many different ways of analysing mark-recapture or mark-recovery data (Lebreton *et al.* 1992, Williams *et al.* 2002, Sandercock 2003). Whether birds are re-encountered dead or alive represents a fundamental dichotomy for analysis of survival rates. Although methods are being developed which combine both (e.g. Kendall *et al.* 1997, Barker 1999), the two approaches have very different biases and, consequently, analytical techniques. In areas where ringing occurs at more than one site, multi-strata models may be required to model capture heterogeneity in the dataset.

Problems with heterogeneity in the data tend to be greater for re-sight/re-capture models than recovery models and goodness of fit testing is essential to explore these issues prior to any analysis. Dead recoveries have the advantage that although reporting rates may be low, effort is generally spread out over a large geographical area, thus reducing bias in reporting rates, though the spatial distribution of recoveries may also show biases. In contrast, live recoveries (controls), especially when using cannon nets tend to occur on few occasions and are limited to a very specific geographical area. Waders are often very site-faithful (Rehfisch *et al.* 1996), thus birds caught only a few hundred metres apart may have very different recapture probabilities.

For survival analyses the software of choice is MARK (White & Burnham 1999, *http://www.cnr.colostate.edu/~gwhite/mark/mark.htm*) though other packages, such as SURVIV and SURGE are available (try *http://www.mbr.nbs.gov/software.html*). For multi-state models M-SURGE may be the best option (*ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/M-SURGE/*). U-CARE (*ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/U-CARE/*) may prove useful for goodness of fit testing.

Example studies

Eurasian Oystercatcher *Haematopus ostralegus*: Goss-Custard (1996), Atkinson *et al.* (2003); Red Knot *Calidris canutus*: Boyd & Piersma (2001), Atkinson *et al.* (2003); Eurasian Golden Plover *Pluvialis apricaria*: Jukema *et al.* (2001), Piersma *et al.* (2005).

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APPENDIX 2. MONITORING SURVIVAL: COLOUR-MARKING

Summary

Outline of method

Colour marking consists of catching and marking a sample of birds and fitting each with a unique combination of coloured rings or flags (which may have a unique combination of characters inscribed). Survival rates are estimated from re-sightings of marked birds.

Advantages

The method needs a relatively small number of individuals to be marked, as re-encounter rates tend to be high (often over 75%). Re-sighting can sometimes be done simultaneously as assessing the proportion of juveniles in the field. Birdwatchers and other naturalists can contribute sightings from throughout the species range.

Disadvantages

Where re-sighting only occurs locally, only apparent survival can be estimated. Observers must get close enough to birds to see combinations reliably. Periods in which conditions are suitable for ring re-sighting may be short and rings can be hard to see. Time and a certain amount of skill are required to read combinations successfully in difficult field conditions. Sightings from birdwatchers may not be reliable and much time is required to administer a scheme and provide feedback.

Method

Birds are caught with cannon nets, mist nets or walk-in traps and are then marked with a unique combination of coloured rings or flags (which may have a unique alphanumeric code inscribed). It is recommended that a metal ring is also put on, so that the bird can be reported if found dead. The material and colours used for the rings or flags must be sufficiently stable to last the lifetime of the study. Use photo-stable materials such as some types of 'Darvic'®; do not use celluloid. It is advisable to 'glue' the rings with a suitable solvent or weld the ends with a solder gun. Because waders do not recognise political boundaries, it is essential that schemes be designed in consultation with the appropriate colour mark registrar (Table 1). Because of their very low survival rates, individual colour marking of chicks, except when close to fledging, is not normally recommended (as many combinations will be rapidly 'lost'); cohort marking of chicks may generate useful sightings away from the breeding grounds.

Reading errors can be frequent with colour-ring combinations, though training helps a great deal (Ward 2000, Milligan *et al.* 2003). In some species it is difficult to see marks above the 'knee', whilst on others marks below the 'knee' are often covered in mud or obscured in water. Use bold, easily differentiated colours – some can be difficult to distinguish at a distance e.g. blues and greens, pale blue and white. Rings may fade (e.g. reds may resemble orange) or discolour over time (e.g. white resembles yellow) (e.g. Collins *et al.* 2002 and refs therein). Experience is the best guide in identifying these problems, though experiments using decoys observed at a distance with telescopes to try out various combinations of rings and colours may also be helpful.

The commonest error, even amongst experienced observers, is transposing left and right legs; avoid using combinations that are mirror images until other combinations are exhausted. When using inscribed rings or flags, the colours used should provide good contrast for the lettering, which should be in a clear, wide, font for maximum readability (Clark *et al.* in prep). Finally, check personnel are not colour-blind.

Site characteristics

Before starting a colour-ringing programme, be certain that you will be able to regularly check a substantial proportion of the birds on the site ideally in all locations, as birds may be faithful to relatively limited areas. Observing feeding birds may be more successful than roosting birds and may be necessary to ensure all birds have an equal probability of re-sighting (Bearhop *et al.* 2003). Colour marking will be most useful when birds can be viewed at sites throughout the migratory cycle.

Sampling period

For monitoring a population, the period during which birds are ringed and subsequently re-sighted should occur when most individuals are resident within an area to be effective. Avoid times with high emigration and immigration or when only a small percentage of the eventual population is present. Re-sightings, though, should be encouraged all year as the additional information can help produce more accurate survival rates (rather than just return rates). To fully understand the causes of population change it may also be necessary to mark individuals in breeding or staging areas.

Minimum annual sample size

In order to obtain good survival rate estimates, sightings of at least 50 marked birds per year are likely to be required (Fig. 1). Successful colour mark studies typically achieve re-sighting rates of 60% or more, thus it is likely that a minimum colour-marked population of at least 100–150 birds will be required, but this will vary with the ease with which a species is resighted and the frequency that observers visit suitable sites. Resighting effort should be distributed across the site in proportion to the number of (all) birds present to account for non-random distribution. A systematic sampling regime will be required to ensure a sufficient resighting effort.

Resources required

Following initial capture, significant extra time is required to colour mark birds (which may limit the number of birds which can be marked on each occasion). Ideally, a team of three is required: a scribe (to keep track of combinations) and two people to fit the marks and glue them. Maintaining a spreadsheet of all possible combinations makes deciding on which combination to use on each bird easier. These must be agreed beforehand (Table 1). Subsequent to the capture event, several dedicated and trained people may be required read colour rings in the field. Substantial time investment is required to maintain a colour mark scheme and to respond to sightings from members of the public.

Data analysis

There are many different methods for estimating survival from mark re-sighting data (e.g. Lebreton *et al.* 1992, Williams *et al.* 2002, Sandercock 2003). See Appendix 1 for some general comments on survival analyses, though colour mark studies suffer from a number of additional problems (Bearhop *et al.* 2003).

Example studies

Black tailed Godwit *Limosa limosa*: Gill *et al.* (2001); Eurasian Oystercatcher *Haematopus ostralegus*: Goss-Custard *et al.* (1996), Verhulst *et al.* (2004); Redshank *Tringa totanus*: Burton (2000); Red Knot *Calidris canutus*: Brochard *et al.* (2002).

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APPENDIX 3. MONITORING RECRUITMENT: COUNTS OF PROPORTION OF JUVENILES IN THE FIELD

Summary

Outline of method

This method relies on counting the proportion of individuals within flocks that are juvenile (based on plumage characters) to obtain an index of recruitment of young birds into the population. In some cases, where adults and juveniles have distinct migration timings or occur in different areas, simple counts of entire flocks may be sufficient.

Advantages

This method does not require that birds be caught and consequently requires only one or two people to conduct counts. The sampling program is also less prone to interruption from such as adverse weather. This method can often be done at sites where other methods are not possible, providing the birds are reasonably visible.

Disadvantages

The method only works on species that have a distinguishable juvenile plumage at the time of sampling. Observers also need to get sufficiently close to age the majority of birds and it is possible that the proportions of adults and juveniles may be biased when juveniles in advanced stages of moult are missed.

Method

Observers work systematically through flocks, ageing, if possible, all birds they come across and noting those whose age cannot be determined and total flock size. Even experienced observers should run a few trials each year when fresh juveniles begin to arrive, so they have recent experience with the plumages being sought before recording data. Photographs are a valuable resource in this kind of study. However, a large proportion of those published are taken on staging areas; juveniles on non-breeding grounds will have more worn plumage, or be in the early stages of post-juvenile moult. Worn juveniles can have a very difference appearance having lost most of those pretty rufous markings; look for the distinctively shaped dark feather centres on the upperparts. Build up a collection of photos of young birds at the site being investigated (digiscoping is a relatively cheap way to do this).

At wintering sites

Where juveniles have distinct wintering areas it may be possible simply to count the numbers of birds occurring in such areas. It should be borne in mind that the distribution of birds may be highly dynamic, and influenced by many factors (e.g. van der Have *et al.* 1984, Hilton *et al.* 1999), so it may be necessary to count over a large area. Ideally, all individuals in all flocks should be counted and each individual only counted once on any sampling occasion. Beware of repeatedly counting individuals in the same large flock in consecutive scans, for example, if the flock has been disturbed by a raptor. A general aim might be to age as many birds as there are in the flock, though this might take several scans (if the flock has not been disturbed do not simply go back to the beginning). It is also important to note the total number of birds in the flock, so ratios can be combined from different flocks.

On staging sites

Similar methods apply, but since adults and juveniles in many species migrate more or less separately from each other in time (and sometimes even in space) and hence are influenced by different weather etc., using counts (or catches) of juveniles alone may be more feasible. Furthermore, the sampling effort should be consistent between years or (more realistically) controlled for in analyses.

At migration termini

Occasionally, when populations are high birds may spend the boreal winter outside their normal range. These will often be juvenile birds, so their presence and numbers may provide an index of recruitment. Years of good productivity can be assessed by the presence of birds at unusual sites, or in unusual habitats, these will normally be juvenile birds that are unable to compete for resources at more traditional sites.

Site characteristics

Counts should be made at a representative range of sites, though the need to achieve sufficiently close access to the birds may limit what is practical.

Sampling period

Counts should be made during a period with limited turnover of passage birds. There may be quite a narrow window of opportunity to aim for in such studies. When juveniles arrive, they are in a readily identifiable juvenile plumage but may start to moult into first winter plumage soon after arrival. However, juveniles do not all arrive at the same time and some may be arriving when earlier arrivals have quite advanced post-juvenile moult. The ideal is therefore to aim for the latest time of year at which you are confident that you can pick out all juvenile birds seen (including those in post-juvenile moult). If young birds become indistinguishable from adults before the latest juveniles arrive, it may still be possible to collect data that allows you to compare age ratios from year to year – provided you are consistent in the time of year in which you collect data, though note the timing of migration may vary between years.

In species with delayed maturity (a common phenomenon in the southern hemisphere) there can be a second window of opportunity. For example, Red-necked Stint *Calidris ruficollis* and Curlew Sandpiper *C. ferruginea* adults spending the boreal winter in Australia moult into breeding plumage in March and April, whilst immatures do not; they remain on the non-breeding grounds (Minton *et al.* in press). So for the short period before some adults begin to depart on northwards migration, it is possible to pick out all adults on incoming breeding plumage. Unless the timing of migration and moult is well known for a species in the area, pilot work will be necessary to establish if this method will prove useful.

Minimum annual sample size

On any sampling occasion at least 30–50, but preferably more than 100, birds should be counted to obtain a reasonable estimate of the proportion of juveniles present. Where possible, multiple scans of the flock may be useful to get a good feel for the age-ratio present, particularly if viewing conditions make ageing difficult, however double-counting should be avoided as some individuals are likely to be more observable than others. Where counts of juvenile flocks are made, the aim should be to accurately estimate the size of the entire population. Counts should be made on at least three occasions in a season.

Resources required

Few: a dedicated individual with a telescope and a notebook (or preferably a pre-printed data form) or a tape recorder are the minimum. Note, however, that voice recordings need to be transcribed at a later stage. A scribe to write down counts so the observer does not have to lose eye contact with the flock (and to keep the counter company!) is extremely useful.

Data analysis

Where counts are made of proportions, it is necessary to take account of the binomial nature of the data and this most easily done using general linear models which are readily fitted in most statistical packages (Appendix 4; Crawley 1993, Clark *et al.* 2004).

Example studies

International Shorebird Survey www.shorebirdworld.org/template.php?g=13&c=11; OSNZ Arctic wader project http://osnz.org.nz/nzwaderstudy.htm#juv; Rogers *et al.* (2004).

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APPENDIX 4. MONITORING RECRUITMENT: AGE-RATIOS FROM CATCHES

Summary

Outline of method

The proportion of juveniles in catches of birds made on the non-breeding grounds provides an index of recruitment into the non-breeding population.

Advantages

Ageing in the hand is often easier than in the field, and this method may be possible when birds cannot be aged reliably in the field. This method can be combined with survival monitoring (Appendix 1) in population studies.

Disadvantages

This method actually measures recruitment into the catchable population, so both adults and juveniles need to winter in the same flocks. Further, the proportions of adults and juveniles obtained from different catching methods (e.g. cannon-netting and mist-netting) are not directly comparable.

Method

The catching method needs to be appropriate to the sites monitored, and will typically involve either mist netting or cannon-netting to ensure that a sufficient number of birds are caught (e.g. Minton 2003, Clark *et al.* 2004). Ideally, a single catching method will be used to ensure comparability, as the proportion of juveniles caught differs between cannon netting and mist netting (Pienkowski & Dick 1976) so requiring the use of 'correction' factors. These factors need to be established by catching with multiple methods over the same period of time at a site. Given that there is likely to be much heterogeneity in the distribution of adults and juveniles within and between flocks (e.g. Harrington 2004), multiple smaller catches are likely to be more representative than a few bigger catches.

Site characteristics

Both adults and juveniles must winter on the site, and changes in the proportion of juveniles should reflect changes in recruitment, not changes in winter area. Ideally adults and juveniles should occur in mixed flocks, or at least should be equally likely to be caught. If catches are made on multiple sites, the pattern of catching on each site should be similar between years.

Sampling period

Sampling needs to be representative through time and should avoid periods of high turnover, when birds are arriving and departing from the site. It is necessary to be able to age most birds caught, which may become difficult towards the end of the season. Care needs to be taken when the sexes differ in the ease with which they can be aged.

Minimum annual sample size

As with estimating any proportion reliably, a good number of birds need to be caught on each occasion; 30–50 birds is probably a good figure to aim for, though this will depend to some extent on the number of birds present. Aim for at least three capture occasions each season.

Resources required

As in the survival analyses with ringed individuals (Appendix 1), a substantial effort both in terms of people and time are required on an annual basis to capture a sufficient number of birds. This effort must be sustainable in the long-term to ensure the use of consistent capture methods and intensity.

Data analysis

The basic data required are number of birds aged, which is not necessarily the same as number of birds caught, and the number of juveniles present. In analysing such proportional data, it helps to think of each bird as an individual trial, which may be either 'successful' (a juvenile) or not (an adult). The data are thus binomial in form and can be modelled using generalised linear models (GLM, Crawley 1993, Clark *et al.* 2004). In many cases, the data will not be strictly binomially distributed, site and habitat differences will introduce extra variability, so an over-dispersion term (or scaling factor) is necessary to more accurately compute standard errors and confidence limits. In general, specifying a GLM with a binomial error distribution (because the variability about an estimate depends on the estimate itself) and a logit link function (to keep the estimate of juvenile proportion between 0 and 1) will be appropriate. Such models can be straightforwardly fitted in most statistical packages currently available.

Example studies

Minton *et al.* (2004), Minton (2004); Red Knot *Calidris canutus*: Boyd & Piersma (2001); Dunlin *C. alpina*: Clark *et al.* (2004).

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APPENDIX 5. MONITORING RECRUITMENT: REVERSED RECAPTURE HISTORIES

Summary

Outline of method

The encounter histories used in survival analyses allow the numbers of birds leaving the population to be estimated through mortality or permanent emigration. However, the encounter histories can also be reversed to estimate the number of birds entering the marked population (Pradel *et al.* 1997). The comments on monitoring survival by metal ringing (Appendix 1) apply equally here.

Advantages

One of the major advantages of using this method is that recruitment (births and permanent immigration) and its associated variance can be directly estimated without counting juveniles, or indeed performing any counts at all. The method can also provide direct estimates of population growth rates.

Disadvantages

Recruitment models require large numbers of birds to be caught and have the same issues associated with metal- and colour-ring survival analyses, the most problematic being that the sampling should be unbiased. Unlike Cormack-Jolly-Seber (CJS) models, it is not possible to include age effects into the models and these should be estimate by constructing different datasets based on the birds' age.

Method

Birds are caught and recaptured using cannon-nets or mist-nets (to ensure sufficient numbers), as for survival monitoring (Appendix 1). Capture histories of individual birds are read from the last observation backward through time, rather than from the first observation forwards as is usually done. In this way, when an animal ceases to be observed in the capture history it may on the site for the first time, or may have been present but not observed. Entry of birds into the site (population) thus becomes the main target of the analysis. Using this method of estimating recruitment can be advantageous when there is an age-biased distribution of birds. For example, larger estuaries in the United Kingdom tend only to support adult Grey Plover *Pluvialis squatarola*, whereas rocky shores tend to support a much higher proportion of juveniles. Clearly, a study of populations on the larger estuaries will not be able to estimate recruitment into that population by counting flocks and estimating the proportion of juveniles and recruitment models are a much better way to obtain estimates of recruitment.

Data collection/analysis

The data used is essentially the same as that for estimating survival from metal-ringed birds, except that the capture history is reversed. This method is susceptible to bias and it is also more difficult to correct for this than in conventional CJS analyses. It is extremely important that the study area remains the same, as otherwise the population would be expanding or contracting. It is also very important to check whether there is significant trap response occurring. This can take the form of 'trap happiness' (some individuals are captured more often than expected) and transience (some individuals are less likely to be encountered after initial capture). The models can be easily constructed in MARK (http://www.cnr.colostate.edu/~gwhite/mark/mark.htm).

Example studies

Flamingos *Phoenicopterus* spp.: Pradel *et al.* (1997); Audouin's Gull *Larus audouinii*: Oro & Pradel (2000); Cormorant *Phalacrocorax carbo*: Frederiksen & Bregnballe (2001); Red Knot *Calidris canutus*: P.W. Atkinson unpubl.